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POSSIBLE TRENDS IN ALGAE ADAPTATION TO ENVIRONMENTAL TEMPERATURE REGIME - RESULTS OF COMPUTER EXPERIMENTS

By V.G. Il'ichev

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Model analysis of the microevolution of algae to the environmental temperature regime have shown that the optimal temperatures for species are closely connected with critical points in the environmental temperature.

The Earth's climate is one of the chief factors governing the evolution of the biosphere. In particular, the periodic fluctuations in the planet's thermal regime that occurred in the past caused radical changes in the structure of biocoenoses. At the present time, according to climatologists (Betten, 1985), there exists a real possibility of a substantial transformation in the Earth's climate both as the result of the anthropogenic pollution of the atmosphere (cooling), as well as the development of a "hothouse effect" (warming up). These phenomena can lead to a marked deformation of the annual thermal regime of the planet. It is not impossible that the temperature curve will have a whole series of local extrema in addition to global ones.

These events will lead to a considerable transformation in the structure and functional conditions of biocoenoses. It is to be expected that the most rapid and pronounced transformation will occur at the lower trophic levels of

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the ecological systems - algae, microorganisms, etc. (Pechurkin, 1978).

An important biological characteristic of algal development is the temperature tolerance range. Observations have shown that those species dominate whose optimal temperatures are close to the extrema of the temperature curve in the body of water. For example, the seasonal temperature variation in Taganrog Bay (Sea of Azov region) represents a sine curve with a minimum of 0-4° and a maximum of 25° (Bronfman et al., 1979). At the same time, the optimal temperatures for diatoms and blue-green Azov algae are respectively in the 0-4° and 24-26° ranges (Gorstko et al., 1977).

Generally, however, it is not clear whether this coincidence forms a pattern or whether it is due to other factors. In particular, what deformations can occur in the dynamics of phytocoenoses in the case of change in the contemporary temperature regime of bodies of water?

Various methods may be employed in the investigation of this problem. These include experimental ones, which consist in the creation of artificial complex thermal regimes in laboratory aquacultures and observation of the corresponding microevolution of the algae, as well as theoretical ones, based on mathematical analysis of models of the algal microevolutionary process under the influence of the temperature factor.

In this work are presented the results of a theoretical investigation that refines the above thesis of a relationship between critical points of the temperature curve and optimal temperatures for dominant algae species. The patterns established here (hypotheses) undoubtedly require further experimental verification.

WHAT ARE THE OPTIMAL TEMPERATURES FOR DOMINANT SPECIES?

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In this section, on the basis of model experiments, a hypothesis will be formulated as to a relationship between the optimal temperatures of dominant species and the environmental temperature regime.

Let us first specify the major premises on which is based the mathematical model of the dynamics of competing species.

Let us specify a sufficiently large set of species $\{x_1, \ldots . x_n\}$. Each species x_i is characterized by its own temperature tolerance range $[\tau_i - \varepsilon, \tau_i + \varepsilon]$ where ε is small. With respect to the tolerance ranges, we shall assume the following: a) adjacent intervals do not intersect and abut each other $\tau_i + \varepsilon = \tau_{i+1} - \varepsilon$ (compact packing of species); b) the combining together of all intervals completely covers the range of environmental temperature change (absence of physiological limitations).

Note that the first assumption corresponds to MacArthur's dense packing principle for evolutionally mature coenoses (MacArthur, 1969, 1970; see also Svirezhev, Logofet, 1978). The second assumption is correct at least for the lower organisms. In fact, microorganisms have shown great adaptational potentials to both high and low temperatures (Aleksandrov, 1975; Lyakh, 1976).

Let us specify an environmental temperature $\theta = \theta(t)$, a smooth periodic function of time and T, its period. In this case, we shall consider that the rate of growth of the ith species is governed by the formula

$$\beta_i(\Theta) = \begin{cases} h, & \text{if } \Theta \in [\tau_i - \varepsilon, \tau_i + \varepsilon], \\ 0, & \text{if } \Theta \bar{\in} [\tau_i - \varepsilon, \tau_i + \varepsilon], \end{cases} \tag{1}$$

Here it would be reasonable to assume that the inequality $2\varepsilon \cdot h/T > 1$ applies - the condition for the nonextinction of the isolated species. Since the parameters of growth (ε and h) are identical for all species, the model species are

"equivalent" if the temperature curve is not specified in advance. Further, the assumed shape of the $\{\beta_i\}$ functions - a thin rectangle - corresponds to the narrow specialization of species developing in their own small temperature range. Such a population structure, after F. Dobzhansky (1970), is called flexible polymorphism.

Let the environmental temperature be the main governing factor. Then the dynamics of the competing relationships can be described by the following system of equations (Contois, 1959; Il'ichev, 1982a,b, 1985):

$$k\dot{x}_i = x_i\left[-\alpha_i + \beta_i(\theta)\cdot p/\left(p + \sum_{j=1}^{n} x_j\right)\right], \qquad (2)$$

where $i = 1, n$; $\theta(t) = \theta[t+T)$; k is a positive parameter describing the "force" of the competing relationships. If k is large ($k \gg 1$), then competition is strong; if k is small ($k \ll 1$), the competition is weak; $\beta_i(\theta)$, α_i are the rate of growth and mortality of the ith species; p is the magnitude of the forage resource, for example, phosphorus.

Below we shall assume that p and $\{\alpha_i\}$ are constant in value with $p \equiv 1$, $\alpha_i \equiv 1$.

In the computer experiments, the following parameter values were taken in the model (2): $n = 250$, $\varepsilon = 0.005$, $h = 1204$, $\gamma_i = 0.01 \cdot i$. Calculations were done at different k values ($k = 1$ and 0.1).

The computer claculations showed that when positive initial values of the variables $\{x_i(0)\}$ are specified in system (2), then as t increases, the trajectories of this model tend to some stable periodic (T is the period) state. This asymptotic condition is singular and does not depend on the choice of the initial vector $\{x_i(0)\}$.

Let us denote by $\bar{x}_i$ the average biomass over the period of the ith species /698

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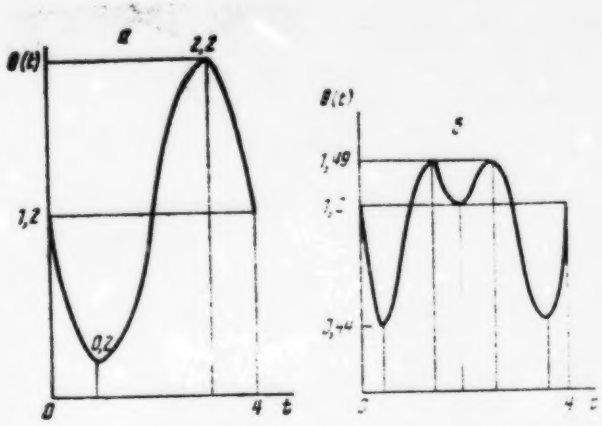

Fig. 1. Temperature curves of the environment in experiments 1(a) and 2(b).

in the asymptotic condition of the model (2). Note that the relation

$$k\bar{x}_i = \frac{1}{T}\int_0^T \beta_i(\theta(t))\,dt - 1. \tag{3}$$

is correct for the dynamics of a single (isolated) species.

We shall reformulate the problem posed above: to determine from a given $\theta = \theta(t)$ curve the optimal temperatures of the dominant species, that is, the species with a (relatively) high average-annual biomass.

Depending on the particular representation of the $\theta = \theta(t)$ functions, the following results have been obtained:

Experiment 1. $\theta(t) = 1.2 - \sin(\pi t/2)$. The graph of this function, which has one minimum $\theta_{min} = 0.2$ and one maximum $\theta_{max} = 2.2$ is shown in Fig. 1, a and is qualitatively similar to the annual temperature variation in the bodies of water. Calculations of the asymptotic condition showed that at $k = 1$, species with optimal temperatures $\tau_{20} = 0.2$, $\tau_{21} = 0.21$ and $\tau_{220} = 2.2$ clearly dominate.

The biomasses of these species are respectively equal to $\bar{x}_{20} \approx 7.58$, $\bar{x}_{21} \approx 9.83$, $\bar{x}_{220} \approx 16.68$ (the biomasses of the other species, by contrast, are low ≈ 0.0004). At $k = 0.1$, in addition to the previous dominants $\{x_{20}, x_{21}, x_{220}\}$ there also exist other species with rather large biomass $(x_{26}, x_{41}, x_{214})$. However, the biomass of the latter species is still substantially smaller than that of the former.

On the whole, this model experiment allows us to formulate two plausible hypotheses.

Hypothesis 1, or the hypothesis of maximal dispersal. The dominant species are situated at the two opposite ends of the temperature ecological niche.

Hypothesis 2, or the critical points hypothesis. The optimal temperatures of the dominant species coincide with the critical points of the temperature curve.

Remember that the temperature value τ is called critical if τ is a an internal local minimum or maximum of the function $\theta(t)$. Formally, there exists a t such that $\theta(t) = \tau$ and $\dot{\theta}(t) = 0$.

Obviously, these hypotheses will give an identical result for a sinusoidal enivornmental temperature curve.

Let us present a model experiment which refutes hypothesis 1.

Experiment 2. Let the environmental temperature be specified by the following periodic function (see Fig. 1, b):

$$\theta(t) = 1{,}2 + (t-2) \cdot \sin(\pi(t-2))/2 \text{ with } t \in [-2, 2],$$

while for the other values of $t > 0$, we shall predetermine θ by the formula

$$\theta(t) = \dot{\theta}(t-4).$$

This function has two local minima: $\theta_{min} = 0.439$ and 1.2 and one /699
maximum θ_{max} 1.485.

We shall note first of all that if hypothesis 1 were correct, then only the two most distant species, within the limits of the specified temperature range, with optimal temperatures $\tau_{44} = 0.44$ and $\tau_{149} = 1.49$, should be dominant.

On the contrary, by hypothesis 2, the dominant species should include not only the species with optimal temperatures $\tau_{44} = 0.44$ and $\tau_{149} = 1.49$, but still another species with $\tau_{120} = 1.2$.

The computer calculations showed that at $k = 1$, the species $\bar{x}_{44} \approx 24.08$, $\bar{x}_{120} \approx 7.13$, $\bar{x}_{149} \approx 18.78$ have a high average-annual biomass (the biomasses of the other species are extremely low ≈ 0.0005). At $k = 0.1$, in addition to the previous dominants, other species also have a high biomass although it is substantially lower than that of $\bar{x}_{44}$, $\bar{x}_{120}$ and $\bar{x}_{149}$.

Thus experiment 2 refutes hypothesis 1 on one hand and supports hypothesis 2 on the other.

THE PARADOXICAL PHENOMENA OF STRONG COMPETITION IN A VARIABLE ENVIRONMENT

This section is preliminary to the proof of hypothesis 2. We shall prove here that it is very difficult to substantiate naturally hypothesis 2 in the case of strong competition.

In a constant environment, Gauze's principle of competitive exclusion - two species cannot long exist on the same food resource - is one of the classical results (Gauze, 1935).

In a variable environment, such as with changing temperature, the issue of competition is not clear. It has been shown that competition in a variable enivironment is less strong and allows many species to coexist if their tolerance

intervals (with respect to a given group of factors) do not inersect (Timofeev-Resovskii, Svirezhev, 1966; Armstrong, McGehce, 1976).

This result clearly demonstrates one of the qualitative differences between competition in a variable environment and in a stable one. We shall present as well a series of paradoxical statements, obtained by computer analysis of the mathematical model of the dynamics of competing species in a variable environment (thecalculations were done by I.L. Briskin).

Paradox 1. The short-lived species crowds out the long-lived one. Let us examine a particular case of model (2) - the model of the competition of two species:

$$\begin{cases} k\dot{x}_1 = x_1[-1 + \beta_1(t)/(1 + x_1 + x_2)], \\ k\dot{x}_2 = x_2[-1 + \beta_2(t)/(1 + x_1 + x_2)]. \end{cases} \tag{4}$$

In a constant environment (β_1 and β_2 are constants), the species x_1 displaces the species x_2 if and only if $\beta_1 > \beta_2$.

Now let the environment be a variable one. In the simplest case $\beta_1(t)$ and $\beta_2(t)$ are periodic time functions where $T = 3$ is the period. The graph of each of these β_i functions takes the shape of a rectangle

$$\beta_i(t) = \begin{cases} h, \text{ if } t \in [a_i, b_i] \\ 0, \text{ if } t \notin [a_i, b_i] \end{cases}$$

We shall call the quantity $|b_i - a_i|$ the time of development (life) of the ith species. In this connection, it would be natural to expect that the species x_1 will displace or at least surpass the species x_2 if $\bar{\beta}_1 > \bar{\beta}_2$, where $\beta_i = h \cdot |b_i - a_i|$ is the area of the ith rectangle.

This statement, generally speaking, is erroneous. In fact, let us take rectangular functions with the following parameters:

$$\beta_1: a_1 > 0,\ b_1 = 0.1,\ h = 110;$$

$$\beta_2: a_2 = 1,\ b_2 = 1.11,\ h = 110,$$

and let $T = 3$, $k = 1$. Since the base of the first rectangle is smaller than that

of the second, we then may say that the first species is short-lived, while the second is long-lived. /700

Obviously, $\bar{\beta}_1 < \bar{\beta}_2$. Nevertheless, the computer calculations showed that the first species displaces the second. The reason for this phenomenon lies in the fact that the competitive pressure of the first species on the second is greater than that of the second species on the first. In fact, the distance in time between the first and second is $\simeq T/3$, while that between the second and the first is $\simeq 2T/3$.

Paradox 2. The intransitivity of competition. Let us have a look at the corresponding model of the dynamics of three competing species:

$$\begin{cases} k\dot{x}_1 = x_1[-1 + \beta_1(t)/(1 + x_1 + x_2 + x_3)], \\ k\dot{x}_2 = x_2[-1 + \beta_2(t)/(1 + x_1 + x_2 + x_3)], \\ k\dot{x}_3 = x_3[-1 + \beta_3(t)/(1 + x_1 + x_2 + x_3)]. \end{cases} \quad (5)$$

where the parameters of the rectangular $\{\beta_i\}$ functions are the following:

β_1 : $a_1 = 0$, $b_1 = 0.1$, $h = 110$;
β_2 : $a_2 = 1$, $b_2 = 1.1$, $h = 110$;
β_3 : $a_3 = 2$, $b_3 = 2.1$, $h = 110$,

and let $T = 3$, $k = 1$. Obviously, $\bar{\beta}_1 = \bar{\beta}_2 = \bar{\beta}_3$.

It turns out that this set of functions $\{\beta_i\}$ determines a peculiar dynamic of competing species: a) in the absence of the third species ($x_3 \equiv 0$), the first species displaces the second; b) in the absence of the second species ($x_2 \equiv 0$), the third species displaces the first; c) in the absence of the first species ($x_1 \equiv 0$), the second species displaces the third.

Let us denote by the relationship $x_i \rangle x_j$ that species i suppresses species j. In this example, there will then be a cyclical relationship of competitive "superiority":

$$x_1 \succ x_2, \; x_2 \succ x_3, \; x_3 \succ x_1.$$

In other words, competitive relationships in a variable environment,

generally speaking, are intransitive.

Paradox 3. Stable system consisting of unstable subsystems. The model presented above (5) and the functions $\{P_i\}$ determine still another unexpected property of competition in a changeable environment: a subsystem of any two competing species is unstable (one species displaces the other), while the complete system of species is stable (the three species coexist together).

Consequently, a competitive coenosis, in which diversity is due to the changing nature of external environmental factors, is "fragile", since the disappearance (or destruction) of only one of the populations may result in the "domino-effect" disappearance of other biological species as well.

These examples of paradoxical phenomena 1-3 also hold for other classes of models and demonstrate that the construction of a theory of strong competition in a variable environment represents a complex problem. By contrast, the influence of weak competition in a variable environment is rather natural and does not contain, as a rule, contraintuitive concepts. In particular, with $k \leq 0.1$, paradoxes 1, 2 and 3 do not obtain at all in models (5) and (4).

PROOF AND REFINEMENT OF HYPOTHESIS 2

The paradoxical effects of competition in a changeable environment described above show that it is rather difficult to offer a strict substantiation of hypothesis 2 in the case of strong competition. We shall therefore examine here the simplest case of weak competition on the assumption that the bases of the rectangular $P_i(0)$ functions are narrow.

Let k be small. Then each variable x_i in model (2) takes on very small values outside of its tolerance interval. Since the tolerance ranges of the different species do not intersect, the interspecies competitive interaction is /701

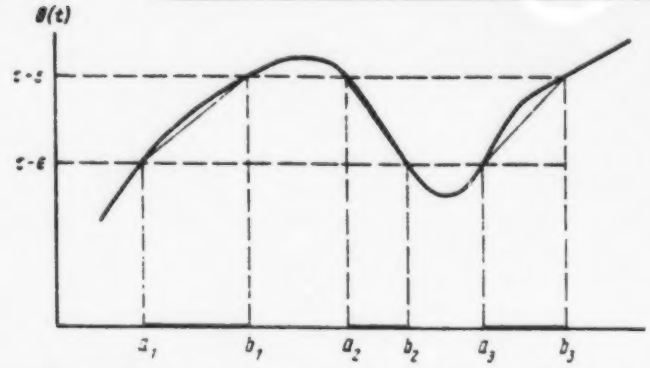

Fig. 2. Relationship between time of optimal algae development and environmental temperature.

weak and the model (2) which relates all the $\{x_i\}$ variables among each other breaks down into n practically unrelated equations of the type

$$k\dot{x}_i = x_i[-1 + \beta_i(\Theta)/(1 + x_i)]. \tag{6}$$

Thus, the problem of determining the dominant species in model (2) amounts to the problem of finding the dominant species in a system of n type (6) equations.

Let us find the explicit estimates of the average-annual biomass of the species x (we shall hereinafter omit the number i), whose development is governed by equation (6). For this, we shall divide the segment $[0,T]$ into m intervals:

$$T_0 = 0 < T_1 < T_2 < \ldots < T_{m-1} < T_m = T,$$

in each interval $[T_j, T_{j+1}]$ the function $\theta = \theta(t)$ is strictly monotone. Then the explicit dependence of the function β on the time t is obtained from simple geometric considerations (see Fig. 2):

$$\beta(t) = \beta(\Theta(t)) = \begin{cases} h, & \text{if } t \in [a_j, b_j] \subseteq [T_j, T_{j+1}], \\ 0, & \text{if } t \in [a_j, b_j], \end{cases} \tag{7}$$

where $[a_j, b_j] = \theta^{-1}([\tau-\varepsilon, \tau+\varepsilon])$ is the constriction of the multivalent inverse function θ^{-1} on the interval $[T_j, T_{j+1}]$. It is obvious that the curve of the

function $\beta(t)$ includes several rectangles with identical height but with different bases. From formula (3), it follows that

$$k\bar{x} = \frac{1}{T}\sum_{j=1}^{m} S_j - 1 = \frac{h}{T}\sum_{j=1}^{m} |a_j - b_j| - 1, \tag{8}$$

where S_j is the area of the jth rectangle and $S_j = h \cdot |a_j - b_j|$.

It remained only to assess $|a_j - b_j|$ at small ε and depending on the nature of τ values. According to Lagrange's theorem, from elementary analysis there exists in the interval $[a_j, b_j]$ a point c_j such that

$$|\Theta(a_j) - \Theta(b_j)| = |\dot{\Theta}(c_j)| \cdot |a_j - b_j|. \tag{9}$$

Rewriting formula (9), we have

$$|a_j - b_j| = 2\varepsilon / |\dot{\Theta}(c_j)|. \tag{10}$$

Let us denote by δ_j the point from the interval $[a_j, b_j]$ for which $\Theta(\delta_j) = \tau$. It follows from the discontinuity of the function $\Theta(t)$ that $c_j \to \delta_j$ as $\varepsilon \to 0$. Moreover, if δ_j is a noncritical point, that is, $\dot{\Theta}(\delta_j) \neq 0$, then

$$|a_j - b_j| \to 2\varepsilon / |\dot{\Theta}(\delta_j)| \text{ as } \varepsilon \to 0. \tag{11}$$

If, on the other hand, δ_j is critical but nonsingular $(\ddot{\Theta}(\delta_j) \neq 0)$ then by Taylor approximation to quadratic terms of the $\Theta(t)$ function in the vicinity of δ_j we may obtain the following relationship: /702

$$|a_j - b_j| \to 2\sqrt{2\varepsilon} / \sqrt{|\ddot{\Theta}(\delta_j)|} \text{ as } \varepsilon \to 0 \tag{12}$$

On the whole, if the value of τ is specified, then the value of $\bar{x}$ can be determined from formulas (7), (8), (9), (10), (11) and (12). In other words, for small ε, there exists a function $\bar{x} \to \bar{x}(\tau)$.

Let us now elucidate at which τ the function $\bar{x}(\tau)$ takes on maximal values.

If τ is a noncritical value of the function $\theta(t)$ then for all δ_j such that $\theta(\delta_j) = \tau$, we have $\dot{\theta}(\delta_j) \neq 0$ and all the terms in formula (8) will be on the order $\sim \varepsilon$. Consequently, $\bar{x}$ will be on the order of $\sim \varepsilon$.

If, however, τ is a critical value of the function $\theta(t)$ (an internal local maximum or minimum), then at least one of the terms in the total (8) will be of the order $\sim \sqrt{\varepsilon}$. Then $\bar{x}$ will be on the order $\sim \sqrt{\varepsilon}$.

Thus, if τ is a critical value of $\theta(t)$ then $x(\tau)$ is a local maximum. In other words, <u>the species x_i is dominant if its optimal temperature τ_i coincides with one of the critical values of the temperature of the environment</u>.

More careful analysis shows that the function $\bar{x}(\tau)$ can take on maximal values at other τ as well. For example, if in the variation of τ, the corresponding magnitudes of $|\dot{\theta}(\delta_j)|$ in the total (8) for all $j \geqslant 2$ vary little, then the value of $\bar{x}$ is determined only by the first term, $2\varepsilon/|\dot{\theta}(\delta_1)|$. Let $|\dot{\theta}(\delta^*)|$ now be the minimal value of the function $|\dot{\theta}(\delta)|$ for $\delta \in [T_0, T_1]$. Then the magnitude $x(\tau^*) = x(\theta(\delta^*))$ is a local maximum, although it still has the order of $\sim \varepsilon$. Formally, this means that one of the following two conditions must be met:

$$\begin{aligned} &1)\ \dot{\theta}(\delta^*) > 0,\ \ddot{\theta}(\delta^*) = 0,\ \dddot{\theta}(\delta^*) > 0; \\ &2)\ \dot{\theta}(\delta^*) < 0,\ \ddot{\theta}(\delta^*) = 0,\ \dddot{\theta}(\delta^*) < 0. \end{aligned} \qquad (13)$$

Thus a local maximum of the function $\bar{x}(\tau)$ can be achieved near some inflection points τ of the function $\theta(t)$. In other words, <u>if the optimal temperature τ_i of the species x_i is an inflection point of the environmental temperature and satisfies the condition (13), then we can expect the species x_i to be dominant</u>.

We shall now cite the following experiments in support of the refined version of hypothesis 2.

<u>Experiment 3.</u> Let the temperature of the environment be specified by the following function

$$\theta(t, c) = 0.1 \cdot [(t-2)^4 - 1.5(t-2)^2 + c(t-2) + 4], \qquad (14)$$

where $t \in [0, 4]$, $\theta(t, c) = \theta(t-4, c)$ and c is a parameter (see Fig. 3, a). Although the function $\theta(t, c)$ is discontinuous at t points that are multiples of 4, this is not of essential importance in the computer experiments. At $c = 1$, this function has a single internal minimum $\theta_{min} \approx 0.25$ and two inflection points $\theta(1.5) \approx 0.31$, $\theta(2.5) \approx 0.42$. The function $\theta(t, 1)$ does not have internal maxima. It is verified directly that the conditions (13) are met only for one of the inflection points. In fact, $\dot{\theta}(2.5) > 0$, $\ddot{\theta}(2.5) \approx 0$, $\dddot{\theta}(2.5) > 0$.

Table 1 shows the results of the computer dynamics of competing species at different k which demonstrate the correctness of the refined hypothesis 2.

<u>Experiment 4.</u> Let the environmental temperature again be specified by the function (14) at another value of $c \approx -1.5$ (see Fig. 3, b). In this case $\theta(t, -1.5)$ has a single internal minimum $\theta_{min} \approx 0.15$ and two inflection points: $\theta(1.5) \approx 0.46$, $\theta(2.5) \approx 0.32$. The function θ does not have any internal maxima. It is not hard to show that only one of the inflection points satisfies the condition (13). In fact, $\dot{\theta}(1.5) < 0$, $\ddot{\theta}(1.5) \approx 0$, $\dddot{\theta}(1.5) < 0$. /703

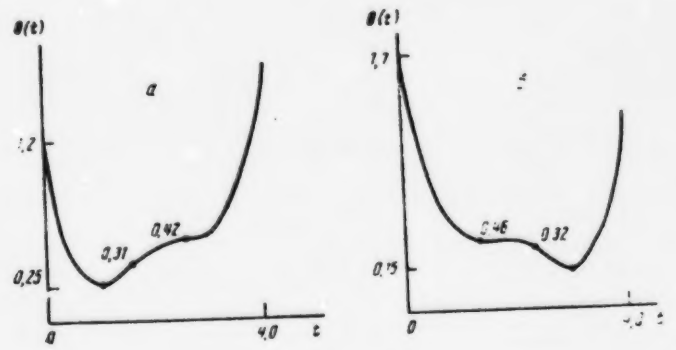

Fig. 3. Temperature curves of the environment in experiments 3(a) and 4(b).

Table 2 shows the analogous results of the computer evolution of the competition of biological species that bear out the refined hypothesis 2.

On the whole, as the results of experiments 1-4 demonstrate, the refined hypothesis of critical points is correct not only for weak but also for strong competition of biological species.

One can discern substantial reasons for the correctness of the critical points hypothesis in the case of strong competition on the basis of the following sufficient sign of absolute dominance (the species x_k is an absolute dominant in a competitive community if it displaces the other species).

"In the model (2), let all $\alpha_i(i=1, k \neq 1$, T be the period of the function $\theta = \theta(t)$ and S_i be the area bounded by the curve of the function $\beta_i(\theta(\tau))$ on the segment $[0,T]$. Then the species x_k is an absolute dominant if $S_k > S_i \exp(T)$ for all $i \neq k$".

Since $S_j \sim \varepsilon$ for the noncritical point τ_j (see (10)) and $S_j \sim \sqrt{\varepsilon}$ for the critical point τ_j (see (11)), then for small ε, the absolute

dominant is as a rule the species for which the optimal temperature coincides with one of the critical points of the environmental temperature.

CONCLUSION

The proof of the hypothesis of the relationship between critical points of the environmental temperature and the optimal temperatures of dominant species was obtained with rather strong biological assumptions. It is therefore fitting at the end of this work to turn once again to the original model premises and discuss their significance for the correctness of this hypothesis.

In the first place, it was assumed that the competitive community represents a wide set of narrowly-specialized species (or subspecies). It is far from all populations (or communities of the same trophic level) that have such a structure. A number of populations are characterized by strong polymorphism, where each individual in the population is broadly specialized. In this case, the critical points hypothesis may not be satisfied.

In the second place, it was assumed in performing the model experiments that the food resource (phosphorus for algae, for example) is constant in time. Such a situation can be achieved in laboratory conditions (flow-through cultivator), but in natural conditions (in bodies of water), the variation of phosporus over time can be so great that it will exert a primary influence on the seasonal productivity of the phytocoenosis. Thus, the spring burst of algae in bodies of water almost coincides with the time of the spring flood. In /704 this case, as well, the second hypothesis may also not be met.

In these exceptional cases, we are dealing not so much with a violation of the critical points hypothesis, so much as the need to modify and refine it to allow for other environmental factors.

The finding of this kind of hypothesis makes it possible in a simple

TABLE 1

Average biomass of species and temperature of the environment θ (t, 1).

k	Некритические точки 1	Минимум $\tau=0,25$ 2	3 Перегибы	
			$\tau=0,31$	$\tau=0,42$
1,0	$\bar{x}_i \leqslant 0,0016$	$\bar{x}_{25} \approx 15,96$	$\bar{x}_{31} < 0,0016$	$\bar{x}_{42} \approx 147,83$
0,1	$\bar{x}_i \leqslant 0,0002$	$\bar{x}_{25} \approx 40,1$	$\bar{x}_{31} < 0,0002$	$\bar{x}_{42} \approx 110,5$

Key:

1 - noncritical points; 2 - minimum of $\tau > 0.25$; 3 - inflection points.

TABLE 2

Average biomass of species and environmental temperature θ (t, -1.5)

k	Некритические точки 1	Минимум $\tau \approx 0,15$ 2	3 Перегибы	
			$\tau=0,16$	$\tau=0,32$
1	$\bar{x}_i < 0,0006$	$\bar{x}_{15} \approx 33,9$	$\bar{x}_{16} \approx 9,7$	$\bar{x}_{32} < 0,0006$
0,1	$\bar{x}_i < 0,00008$	$\bar{x}_{15} \approx 51,0$	$\bar{x}_{16} \approx 6,2$	$\bar{x}_{32} < 0,00008$

Key

1 - noncritical points; 2 - minimum of $\tau \approx 0.15$; 3 - inflection points.

fashion to formulate the main tendencies in the microevolution of the parameters of biological species.

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POSSIBLE TRENDS IN ALGAE ADAPTATION TO ENVIRONMENTAL TEMPERATURE REGIME. RESULTS OF COMPUTER EXPERIMENTS

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The model analysis of the competing species dynamics in changing environment demonstrates that optimal temperatures for dominating species coinside with critical points of environmental temperature.